SOME ASPECTS OF BISON ECOLOGY AND BEHAVIOR IN A TALLGRASS PRAIRIE

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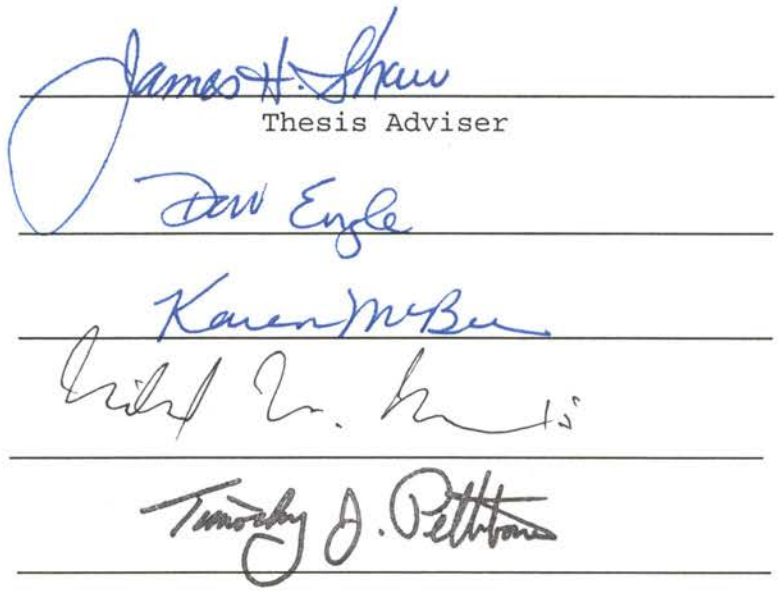

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CHAPTER I

INTRODUCTION

Bison (*Bison bison*) has been identified recently as a keystone species in tallgrass prairie (Knapp et al. 1999). This thesis comprises four studies involving bison and the tallgrass prairie, from seed dispersal to productivity.

Chapters II, III, IV, and V are manuscripts formatted for publication, whereas chapter VI is a summary with the main findings and conclusions of each manuscript. The first chapter, "Seed dispersal by bison in a tallgrass prairie," is a study of the role of bison as disperser agents of seeds, both endogenously and exogenously. The manuscript is formatted for "Plant Ecology," Chapter III, "Behavioral comparisons between bison and cattle on Southern Plains" is a comparison of grazing and active behaviors of bison and cattle in the tallgrass prairie across seasons, with emphasis on effects of ambient temperature on both types of behaviors. The manuscript is formatted for the "Journal of Applied Animal Behavior." Chapter IV, "Sexual segregation and sex ratios in bison (*Bison bison*) and potential impact on North American Great Plains Prairies," is formatted for "Great Plains Research." This study used

differences in diet composition of adult male and female bison and their segregation during most of the year in conjunction with data on sex ratios of bison in parks and preserves in the Great Plains to discuss potential impacts of constrained sex ratios applied on about half of them. Chapter V, "Bison productivity on tallgrass prairie: a comparison with other Great Plains' herds," covers analysis of bison calving rates and weight data collected during seven years at the annual roundups in the Tallgrass Prairie Preserve. The data were compared with data on bison productivity of other Great Plains herds published in the literature to clarify aspects of the theory that bison were scarce in tallgrass prairie regions because of nutritional deficiency. The manuscript is formatted for the "Great Plains Research."

Reference

Knapp, A.K., J.M. Blair, J.M. Briggs, S.L. Collins, D.C. Hartnett, L.C. Johnson, and E.G. Towne. 1999. The keystone role of bison in the North American tallgrass prairie. BioScience 49:39-50.

CHAPTER II

Seed dispersal by bison (*Bison bison*) in a tallgrass prairie

Abstract

To determine the role of bison as seed dispersers in a tallgrass prairie, I collected bison hair samples (n=111) from bulls, cows and juveniles during the fall roundups of 2000 and 2001, and dung samples monthly (n=144) from cow groups during 2001 at the Tallgrass Prairie Preserve, Osage County, Oklahoma. I collected 2,768 seeds from at least 76 plant species in bison hair. Hair samples from bulls, cows and juveniles differed in seed species composition. I found in hair several species that did not feature specialized appendages for adhesive dispersal, which suggest that such species could be benefited by epizoochory as an additional dispersal mode. I found 7,407 seeds from at least 71 species from 23 plant families in dung samples. Species composition of dung samples differed among months. Grass species (Family Poaceae) represented 52.8% of all seeds present in bison dung. A considerable number of forb species were found in bison dung throughout months, indicating that bison could be important dispersers of such species. The great majority of seeds that

were found undamaged in bison dung were small seeds, which is in agreement with the "foliage is the fruit" hypothesis proposed by Janzen (1984).

Introduction

Plant dispersal is an active process of transportation of spores, seeds, fruits or vegetative parts of a plant away from the parent plant, allowing propagules to reach sites to establish a new generation (Fenner, 1985; van der Pijl, 1982). Zoochory, the dispersal of seeds by animals, is potentially directed dispersal because animals select their habitat, increasing the chance that seeds are placed in a habitat similar to that of the parents (Kiviniemi and Eriksson, 1999). Epizoochory is the dispersal of seeds or fruits by adhesion to animal's fur, feathers, or feet. Plants adapted to epizoochory usually have seeds with adhesive mechanisms (spines, hooks or viscid exudates) that facilitate attachment to animal's fur or feathers (van der Pijl, 1982); however, the absence of such mechanisms in seeds does not preclude epizoochory (Fischer *et al.*, 1996).

Endozoochory is characterized by the ingestion of fruits or seeds that pass unharmed through digestive tracts of animals. It is considered adaptive when seeds are adapted to fruit-eating animals and accidental when seeds are indiscriminately ingested with foliage (van der Pijl, 1982). Probably because of that, most studies on endozoochory focused on plants bearing fleshy

fruits and the animals that consume them. However, Janzen (1984) proposed the "foliage is the fruit" hypothesis, suggesting that in small-seeded herbaceous plants, including grasses, the foliage acts as a fruit attracting the disperser agent. This hypothesis has been supported by some studies carried out in Europe and North America (Malo and Suárez, 1995; Quinn et al., 1994).

Seed dispersal can influence species abundance and distribution on local and landscape scales (Kiviniemi and Eriksson, 1999), and seed dispersal has been receiving more attention with the increasing fragmentation of natural and semi-natural habitats. The tallgrass prairie is one of the most endangered and fragmented ecosystems of North America; its range has been reduced to less than 5% of that of presettlement times (Samson and Knopf, 1994). Fire, drought, and bison (*Bison bison*) grazing were major disturbance forces shaping the presettlement tallgrass prairie (Knapp *et al.*, 1999). It is then reasonable to suspect that bison would serve as seed dispersers of plant species on the tallgrass prairie, both by external and internal means. Obtaining information about seed dispersal by bison will increase our understanding of ecological processes occurring in the tallgrass prairie and can improve future actions to conserve and restore remaining tracts of this ecosystem.

The purpose of this study was to determine the importance of bison as agents of dispersal of plant species via epizoochory and endozoochory in a tallgrass prairie. To accomplish this objective, two studies were carried out. In the first study I

examined presence and abundance of seed species in bison hair. Sex may influences seed composition in bison hair because adult male and female bison segregate in different groups during most of the year and show different grazing patterns (Coppedge and Shaw, 1998). Because of that, I tested the following null hypothesis: 1) there is no effect of animal category (bulls, cows, juveniles) in the seed composition of bison hair samples. In the second study I examined the presence and abundance of seed species in bison dung across months and tested the following null hypotheses 2) there is no difference between months in number of seed species in bison dung; 3) there is no difference between months in seed composition in bison dung.

Methods

Study Area

The Tallgrass Prairie Preserve (TGPP) is one of the last tracts under one ownership of tallgrass prairie that remains unplowed in North America. It is owned by The Nature Conservancy and located in Osage County, Oklahoma (36°50'N 96°25'W). *Andropogon gerardii*, *Sorghastrum nutans*, *Panicum virgatum*, *Schyzachyrium scoparium* and *Sporobolus compositus* dominate the vegetation of the area. *Carex* spp. are subdominant graminoids, and *Ambrosia psilostachia* and *Amphiachyris dracunculoides* are common forbs (Coppedge, 1996). Seasonal patch burns are performed annually in about 30% of the preserve which, in

combination with bison activities, create a shifting mosaic of vegetation structure and composition (Hamilton, 1996).

Epizoochory study

During fall the roundup of 2000 and 2001, animals were individually constrained in a squeeze chute and hair samples were collected from each animal's forehead using an electric clipper. I searched the hair samples for attached seeds under a magnified lamp, and placed seeds in envelopes for subsequent counting and identification. To identify seed species, I examined seeds under stereomicroscope using seed identification manuals (Davis, 1993; Delorit, 1970; Martin and Barkley, 1961) and the seed collection of the OSU Herbarium. Seeds that appeared damaged on visual inspection were discarded. Seeds were identified to genus or species level. Seed abundance was expressed on a per gram of hair basis.

I analyzed the data using Redundancy Analysis (RDA), a special type of multiple regression analysis. RDA "is an ordination of the species data in which the axes are constrained to be linear combinations of the environmental variables" (ter Braak and Prentice, 1988). I used CANOCO 4 to perform RDA on the seed data using bulls, cows and juveniles as nominal explanatory variables and year as covariate. I used the default options of CANOCO 4, except that I square-rooted transformed the data. Monte Carlo permutation tests were performed to verify the significance of

all axes. Seeds that were not possible to identify were included in the analysis in three groups: grass seeds, seeds from family Asteraceae, and seeds from unknown family.

Endozoochory study

I collected dung samples from bison (n=12) monthly from January through December 2001 (total of 144 samples). During each collection date I followed the first bison group I met (≥ 10 bison) on foot from the main roads inside the TGPP. I always followed cow or mixed groups, because bulls represented a very small portion of the population. I waited until the animals started moving out and searched the area for fresh dung. I avoided collecting the parts of the dung that were in direct contact with the soil. Dung samples were split into two sub-samples, placed in identified plastic bags, and brought to the laboratory. I weighed about 20 g of each dung sample in a precision scale and let them dry in an oven at 35° C for 24 hours to calculate the dry matter content of each sample. One set of subsamples was preserved at 5° C until it was possible to process them, and the other set was kept at -20° C for posterior germination trials. I washed 50 g of each fresh dung sample under tap water in a set of sieves (1.8 mm, 1.0 mm, and 500 μm screen sizes), placed sieves in a drying oven, and let them dry at about 35° C for 12 to 24 hours. Dry material was removed from sieves and placed in envelopes. Seeds present in the samples

were sorted under magnification, and placed in envelopes. Seeds that appeared damaged under stereoscope inspection were discarded. Seed identification was performed similarly to methods described for bison hair. In addition, to help seed species identification, I thawed a few dung samples that were kept at -20° C from each month, mixed with vermiculate, and germinated them in pots in a growth room under constant light, watering them every other day.

I used both univariate and multivariate methods to analyze the data. I used analysis of variance (GLM procedure of SAS) to test for differences in both number of species per sample and seed abundance in samples (number of seeds per gram of dung dry matter) across months. When F tests were significant (α=0.05) I performed multiple mean comparisons tests using Bonferroni method. Before each analysis I tested the data for homogeneity of variance (Levene's test). Because heterogeneity of variance was detected in seed abundance data, data were log-transformed before performing the analysis.

I used Redundancy Analysis (RDA) to analyze data in Canoco 4 using months as nominal explanatory variables, and performing Monte Carlo Permutation tests. The default options were followed, except when data received a square-root transformation. Seeds that were not identified were included in the analysis in three groups as described for the epizoochory study.

Results

Epizoochory study

I found 2,768 seeds from at least 76 plant species (117 seeds could not be identified) in 111 hair samples from bison in both 2000 and 2001 (Table 1). The most common species occurring in bison hair samples are presented in Table 1. No seeds were found in only two hair samples. The null hypothesis that animal category (bulls, cows, and juveniles) does not influence the composition of seeds present on bison hair was rejected. Monte Carlo permutation tests were significant for both the first (eigenvalue = 0.032, P = 0.0010) and all canonical axes (eigenvalue = 0.054, P = 0.0010). Figure 1 depicts the relationship of seed species with nominal explanatory variables (bulls, cows and juveniles). Length of arrows is associated with species abundance, whereas direction of arrows indicates species association with other species and with environmental variables. A greater number of species (represented by arrows) are positively associated to cows than to bulls or juveniles. Seeds were also more abundant (represented by species length and direction) in cows than in bulls or juveniles' samples. From the most abundant species found on bison hair, *Bromus* spp. and *Elymus* spp. occurred more frequently in the same samples. *Ambrosia artemisiifolia*, *Amphiachyris dracunculoides*, and *Iva anuua* were abundant in samples and negatively related to bulls, whereas *Torilis arvensis* was abundant, highly related to cows, and

negatively related with juveniles. *Xanthium strumarium* and *Andropogon gerardii* were related to juveniles and negatively associated with cows.

Endozoochory study

From 7407 seeds found in bison dung samples, 6970 were identified to at least genus level (70 species from 23 families). Table 2 shows a list with the most common species found in bison dung. Only 2 of 144 samples did not contain any seed and were collected in the month of March. Hypothesis 2 was rejected because months differed in the number of species present in dung samples ($F= 12.52$, $df=11$, $p<0.0001$). February and March had similar number of species per sample ($p=0.1659$) and had less species than all other months (Fig. 2). The highest numbers of species were found in June and July samples (Fig. 2). The abundance of seeds in samples (number of seeds per gram of dung dry matter) also varied among months ($F=28.11$, $df=11$, $p<0.0001$), were minimum in February and March, and maximum in July (Fig. 3).

Monte Carlo tests from Redundancy Analysis (RDA) were significant for the first (eigenvalue=0.116, $F=17.126$, $p=0.001$) and all axes (eigenvalue=0.372, $F=6.999$, $p=0.001$) indicating that months differed in their species composition (rejection of hypothesis 3). Figure 4 depicts the first 2 axes of RDA, with months represented by triangles (centroids) and species by arrows. Species abundance is represented by length of arrows and

the direction of arrows indicates species association with other species and with environmental variables. The distance between nominal environmental variables indicates the degree of similarity in species composition among them.

January, February and March were associated with each other, but not positively associated with any species in particular. The most abundant species occurring in April dung samples were *Capsella bursa-pastoris*, *Carex grisea*, *Carex* spp., *Viola* spp., *Eleocharis* spp., *Krigia cespitosa*, *Hedyotis nigricans*, and *Veronica peregrina*. Dung samples from May were associated with few species, mainly *Poa* spp., *Sphenopholis obtusata*, and unidentified seeds. June, July, and August dung samples had similar species composition and were associated with several species, among them *Physalis* spp. and *Lepidium densiflorum* were the most abundant. Species composition of September dung samples seemed to be intermediate between seed composition of June, July and August samples and seed composition from October, November and December samples. *Bromus* spp. and *Cynodon dactylon* were the most abundant species associated with September dung samples. Seed composition of dung samples from October, November, and December were similar, and the most abundant species associated with these months were *Eragrostis* spp., *Artemisia ludoviciana*, and rough *Sporobolus compositus*.

Discussion

Epizoochory

From all hair samples processed, only 2 of 111 did not contain any seed, indicating that bison commonly serve as agents in the dispersal of seeds in the tallgrass prairie. These findings support the observations made initially by Berthoud (1892) who found seeds from the following genera on bison hair: *Martynia*, *Bidens*, *Glycyrriza*, *Stipa*, *Setaria*, *Elymus*, *Helianthus*, *Euphorbia*, *Rhus*, *Amaranthus*, and *Chenopodium*. Other studies have shown similar numbers of plant species carried on fur or hair of mammals. Seeds of 85 vascular plant species were found in the fleece of sheep in calcareous grasslands of Germany (Fischer *et al.* 1996). Milton *et al.* (1990) found seeds of at least 54 plant species on fleece of sheep in Karoo rangelands of South Africa.

Sampling in this study was limited to hair from the head, where presumably seeds were attached while animals were grazing, wallowing or lying down. This study was limited to the roundup period (fall), the only time when it was possible to have close but safe access to the animals. Other seed composition and abundance probably would be found if other parts of the body were sampled or if sampling occurred during other months of the year. Fischer *et al.* (1996) found the highest numbers of seeds attached to the breast and neck of sheep; the same is possible in bison, but unfortunately, for safety reasons, it was not possible to

sample those bison body areas. Despite this, this study provides a good illustration of the kinds of species that are likely to attach to bison hair and be dispersed in the tallgrass prairie.

Hair samples from bulls, cows, and juveniles differed in seed composition. Sexual segregation and consequent differences in habitat selection between bulls and cows might be the cause, but the fact that female bison have greater hair density than male bison may also provide a partial explanation (Peters and Slen 1964). This is not the only study that shows sexual differences in epizoochory. In Africa, Agnew and Flux (1970) observed that female hares (*Lepus capensis*) carried three times more seeds on their fur than males, probably due to different grooming behavior between sexes. Differences in seed composition between cow and juvenile samples are more difficult to interpret because juveniles remain in cow groups. Possible causes for that could be simply mechanical (juveniles having shorter hair than adults), behavioral (wallowing and rubbing behaviors are more frequent in adults than in juveniles, [Coppedge 1996]), or a combination of these or more factors.

As would be expected, some species with adhesive appendages were abundant in bison hair samples, as *Xanthium strumarium*, *Torilis arvensis*, *Desmodium sessilifolium*, and *Amphiachyris dracunculoides*. However, many abundant species, most of them from families Poacea and Asteraceae, found in bison hair are known to be wind dispersed. Also, seeds that seemed not to possess specific adaptations to dispersal also were found in

considerable amounts in bison hair. These results suggest that seed morphology alone is a poor indicator of the capacity of seeds to be dispersed on bison hair. It is possible that seeds from any species are successfully dispersed by more than one means, even those with specialized modifications for a specific type of dispersal. In his book "The dispersal of plants throughout the world" Ridley (1930) described more than one mode of dispersal for a substantial number of plant species. Lyons (1994) observed that seeds from *Desmodium* spp. were dispersed by other mechanisms beyond adhesion in a tallgrass prairie. Pakeman et al. (2002) observed that several wind-dispersed species were capable of being dispersed by endozoochory.

A considerable number of some introduced species (species not native to U.S.) were found on bison hair, in particular *Bromus* spp., *Cynodon dactylon*, and by *Torilis arvensis*. The importance of bison as dispersal agents of these species is unknown, but the fact that cattle are considered major dispersers of some noxious introduced plants (Clerck-Floate 1997) may indicate that more attention should be given to this subject.

Endozoochory

A substantial number of species (N=71) were found in bison dung samples, of which graminoids represented 27 species with a total of 3916 seeds. The great variety and number of forb seeds in bison dung was surprising because forbs represent a very small

portion of bison diet in tallgrass prairie (Coppedge and Shaw 1998b). Malo and Suárez (1995) found 78, 66, 67, and 52 seed species in dung of cattle (*Bos Taurus*), red deer (*Cervus elaphus*), fallow deer (*Dama dama*), and rabbits (*Oryctolagus cuniculus*), respectively in a Mediterranean *dehesa* between February and August. The mean seed density found in that study in cattle dung was 9.6 seeds per gram of dung dry matter, similar to those described in bison in the present study. Pakeman et al. (2002) studied seed dispersal by rabbits and sheep in eight sites in United Kingdom, finding that a substantial quantity and range of seeds are dispersed by both species, most of them 'weeds', and that this could have a significant effect on the dynamics and species richness of these ecosystems. In addition, among the most abundant species found, three were from genus *Veronica*, which was also abundant in some months in the present study.

The only other endozoochory study in which bison were used as dispersers did not examine seed species naturally occurring in bison dung, but instead tested the germinability of six forage seeds after bison ingestion and digestion (Gökbulak 2002). Results from this study indicated that seed recovery from dung was greatest for seeds with round shape and hard coat, germinability was lower in two treated (ingested seeds) species than in those untreated, and that bison digestion did not break the dormancy of four species. The goal of the study was to test "fecal seeding", a method of seeding that uses herbivores to disperse desirable plant species by feeding them with their

seeds. Fecal seeding by cattle has been studied in *Panicum virgatum* (Ocumpaugh et al. 1996) and in *Eragrostis lehmanniana* (Fredrickson et al. 1997). After finding that germinability of *Buchloe dactyloides* was enhanced after digestion by cattle and that the quality of the foliage was high during seed production, Quinn et al. (1994) suggested that the foliage-is-the-fruit hypothesis could be applied to shortgrass prairies of North America.

Despite several studies that support the foliage-is-the-fruit hypothesis, there is some criticism in relation to the probability of occurring in grasslands. Collins and Uno (1985) alleged that there would be no need of animals dispersing seeds at large distances in the tallgrass prairie because disturbed sites are very common in this ecosystem. This study do not pretend to affirm that all species found in bison dung were adapted to endozoochory; neverthless, the presence of seeds in bison dung indicates that endozoochory could be an important dispersal mode of some species.

Conclusions

Seed dispersal is an important but little known process that affects plant abundance and distribution at local and landscape levels. The present work supports the idea that bison can be important disperser agents of several species in tallgrass prairie. However, how seed dispersal by bison affects local and

landscape vegetation composition is still to be determined. This study provided a start point for following studies on bison seed dispersal in the tallgrass prairie.

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Table 1. List of 47 most common species found on bison hair samples (N=111) at the Tallgrass Prairie Preserve, Oklahoma, in fall 2000 and fall 2001 (Nomenclature follows Kartesz and Kartesz 1980).

Species	Total Number of Seeds	Presence in samples	Family
Ambrosia artemisiifolia	78	23	Asteraceae
Ambrosia trifida	7	4	Asteraceae
Amorpha canescens	6	3	Fabaceae
Amorpha fruticosa	45	17	Fabaceae
Amphiachyris dracunculoides	93	29	Asteraceae
Andropogon gerardii	622	67	Poaceae
Andropogon ternarius	5	3	Poaceae
Andropogon virginicus	3	3	Poaceae
Aster spp.	63	28	Asteraceae
Bidens frondosa	6	6	Asteraceae
Boehmeria cylindrica	94	14	Urticaceae
Bromus spp.[b]	331	65	Poaceae
Carex spp.	5	5	Cyperacea
Cephalanthus occidentalis	71	19	Rubiacea
Chenopodium spp.[b]	4	4	Chenopodiacea
Conium maculatum[a]	7	3	Apiaceae
Cynodon dactylon[a]	10	6	Poaceae
Desmodium sessilifolium	65	26	Fabaceae
Digitaria spp.	6	5	Poaceae
Eleocharis spp.	4	3	Cyperaceae
Elymus spp.	47	30	Poaceae
Eupatorium altissimum	16	6	Asteraceae
Gaura spp.	15	8	Onagracea
Geum canadense	7	7	Rosacea
Grindelia lanceolata	5	4	Asteraceae

Table 1. Cont.

Species	Total Number of Seeds	Presence in samples	Family
Helenium autumnale	38	22	Asteraceae
Helianthus spp.	7	5	Asteraceae
Hordeum pusillum	17	11	Poaceae
Iva annua	65	20	Asteraceae
Lespedeza capitata	4	3	Fabaceae
Melilotus officinalis	16	9	Fabaceae
Panicum spp.	24	16	Poaceae
Panicum virgatum	7	4	Poaceae
Potentilla arguta	5	3	Rosaceae
Ratibida columnifera	5	5	Asteraceae
Schizachyrium scoparium	23	15	Poaceae
Solidago ssp.	102	32	Asteraceae
Sorghastrum nutans	53	29	Poaceae
Sporobolus compositus	15	11	Poaceae
Torilis arvensis[a]	163	36	Apiaceae
Tridens flavus	61	22	Poaceae
Uniola latifolia	13	8	Poaceae
Verbena urticifolia	4	3	Verbenaceae
Verbesina virginica	28	14	Asteraceae
Vernonia baldwinii	114	31	Asteraceae
Vulpia octoflora	6	6	Poaceae
Xanthium strumarium	207	50	Asteraceae

a- Introduced species (not native to U.S.)

b- Genus with some native and some introduced species

Table 2. Alphabetical list of the 42 most common seed species found in bison dung at the Tallgrass Prairie Preserve, Oklahoma. (Nomenclature follows Kartesz and Kartesz 1980).

Species	Number of seeds	Number of samples	Family
Ambrosia spp.	32	13	Asteraceae
Amphiachyris dracunculoides	6	6	Asteraceae
Andropogon ternarius	5	5	Poaceae
Artemisia ludoviciana	335	21	Asteraceae
Bromus spp.[b]	394	94	Poaceae
Capsella bursa-pastoris[a]	112	12	Brassicaceae
Carex amphibola	14	8	Cyperaceae
Carex spp.	166	75	Cyperaceae
Chaerophyllum tainturieri	69	19	Apiaceae
Chamaesyce maculata	37	9	Euphorbiaceae
Cynodon dactylon[a]	1190	87	Poaceae
Cyperus spp.	52	29	Cyperaceae
Digitaria spp.	60	24	Poaceae
Eleocharis spp.	139	27	Cyperaceae
Elymus spp.	7	7	Poaceae
Eragrostis spp.	80	24	Poaceae
Hedyotis nigricans	134	35	Rubiaceae
Hordeum pusillum	10	10	Poaceae
Krigia cespitosa	67	11	Asteraceae
Lepidium densiflorum	60	32	Brassicaceae
Medicago lupulina	156	42	Fabaceae
Melilotus officinalis	13	9	Fabaceae
Oxalis stricta	32	26	Oxalidaceae
Panicum capillare	36	21	Poaceae

Table 2 Cont.

Species	Number of seeds	Number of samples	Family
Panicum obtusum	21	18	Poaceae
Panicum spp.	65	26	Poaceae
Paspalum setaceum	7	7	Poaceae
Phalaris spp.	7	7	Poaceae
Plantago spp.	162	47	Plantaginaceae
Poa spp.	16	12	Poaceae
Rudbeckia hirta	17	6	Asteraceae
Silene antirrhina	38	15	Caryophyllaceae
Solanum carolinense	827	39	Solanaceae
Sphenopholis obtusata	79	11	Poaceae
Sporobolus compositus	1395	61	Poaceae
Symphocaricarpos orbiculatus	46	10	Caprifoliaceae
Torilis arvensis[a]	11	9	Apiaceae
Trifolium spp.	14	8	Fabaceae
Valerianella radiata	12	10	Valerianaceae
Veronica peregrina	806	32	Scrophulariaceae
Viola spp.	40	11	Violaceae
Vulpia octoflora	135	47	Poaceae

a- Introduced species (not native to U.S.)

b- Genus with some native and some introduced species

Figure 1. Bi-plot showing the first two axes of RDA. Nominal explanatory variables bulls, cows, and juveniles (represented by triangles) are plotted with species, represented by arrows.

Ambrarte: *Ambrosia artemisiifolia;* Ambrspp.: *Ambrosia* spp.; Ambrtrif: *Ambrosia trifida;* Amorcane: *Amorpha canescens;* *Amorfrut: Amorpha fruticosa; Amphdrac: Amphiachyris dracunculoides; Andrgera: Andropogon gerardii;* Andrvirg- *Andropogon virginicus;* Arteludo: *Artemisia ludoviciana; Bidefron: Bidens frondosa; Bromspp.: Bromus* spp.; Cephocci: *Cephalanthus occidentalis;* Chaetain: *Chaerophilum tainturieri;* Chenspp.: *Chenopodium* spp.; *Conimacu: Conium maculatum; Desmosess: Desmodium sessilifolium; Eleospp.- Eleocharis* spp.; *Elymspp.: Elymus* spp.; Eupaalti: *Eupatorium altissimum;* Gaurspp.: *Gaura* spp.; Geumcana: *Geum canandese;* Ivaannu: *Iva annua; Lespcvirg: Lespedeza virginica; Melioffi: Melilotus officinalis;* Monaspp.- *Monarda* spp.; Mononutt: *Monolepis nuttalliana; Panissp.: Panicum* spp.; Planspp.: *Plantago* spp.; Raticolu: *Ratibida columnifera;* Rumespp.: *Rumez* spp.; Salvazur: *Salvia azurea; Sorgnuta: Sorghastrum nutans;* Sporcomp: *Sporobolus compositus; Toriarve: Torilis arvensis; Verbvirg: Verbesina virginica; Vernbald: Vernonia baldwinii;* Unidaste: *Unidentified Ateracea seeds;* Unidgras- *Unidentified grass seeds;* Unidseed: *Unidentified seeds.*

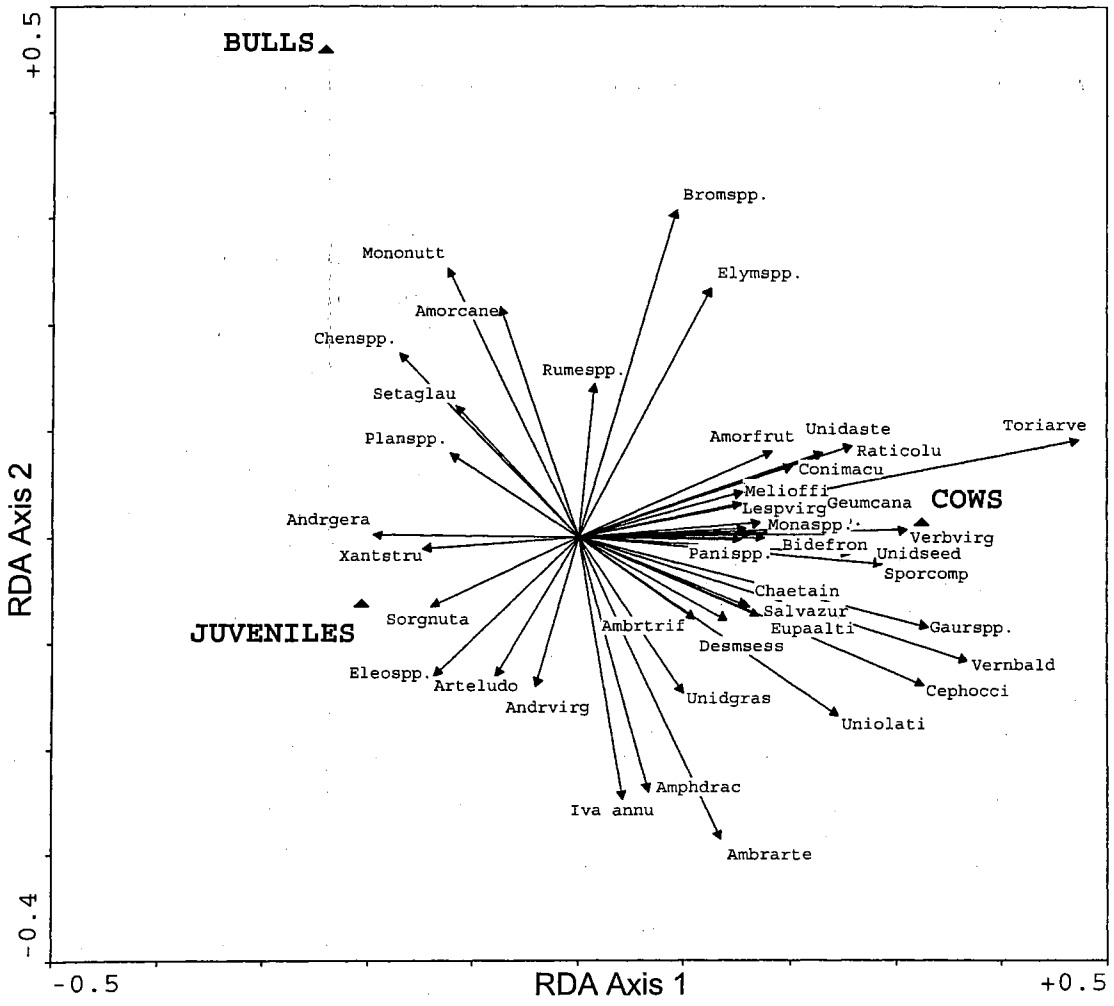
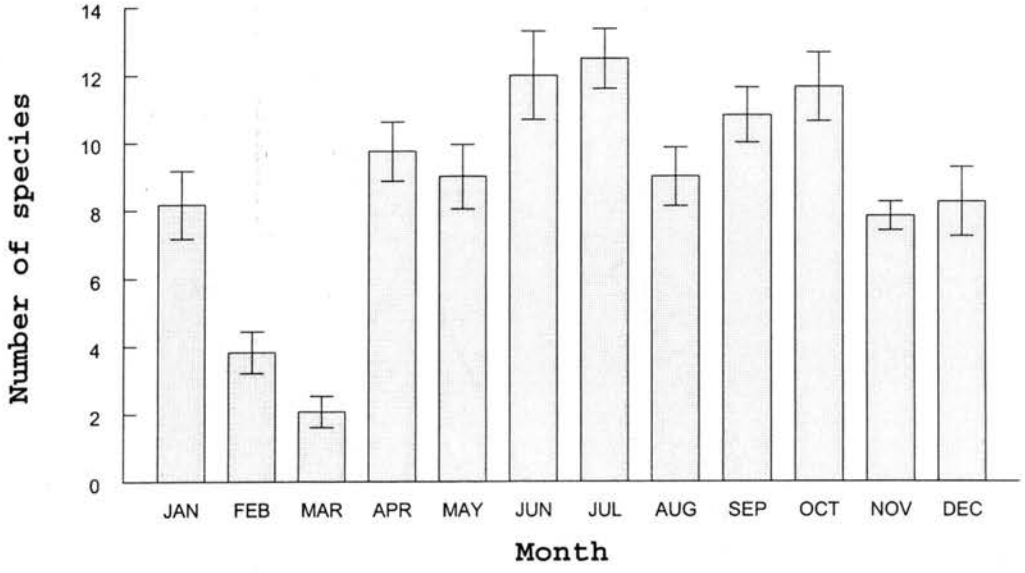

BULLS
COWS
JUVENILES
Bromspp.
Mononutt
Elymspp.
Amorcane
Chenspp.
Rumespp.
Setaglau
Planspp.
Amorfrut
Unidaste
Toriarve
Raticolu
Conimacu
Melioffi
Lespvirg
Geumcana
Monaspp.
Verbvirg
Andrgera
Xantstru
Panispp.
Bidefron
Unidseed
Sporcomp
Chaetain
Salvazur
Sorgnuta
Ambrtrif
Eupaalti
Gaurspp.
Desmsess
Vernbald
Eleospp.
Arteludo
Andrvirg
Unidgras
Cephocci
Uniolati
Amphdrac
Iva annu
Ambrarte
+0.5
-0.4
RDA Axis 2
-0.5
RDA Axis 1
+0.5

Figure 2. Number of seed species (Mean ± S.E.M) per bison dung sample by month.

Figure 3. Abundance of seeds (number of seeds per gram of dung dry matter - DM) (Mean ± S.E.M) in bison dung samples by month (untransformed data).


Number of species
14
12
10
8
6
4
2
0
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
Month

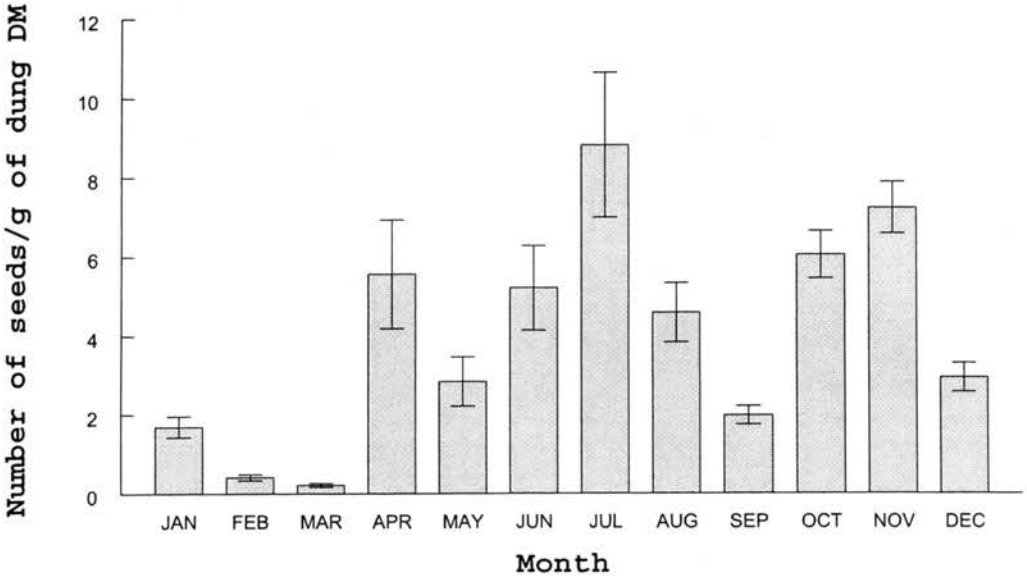
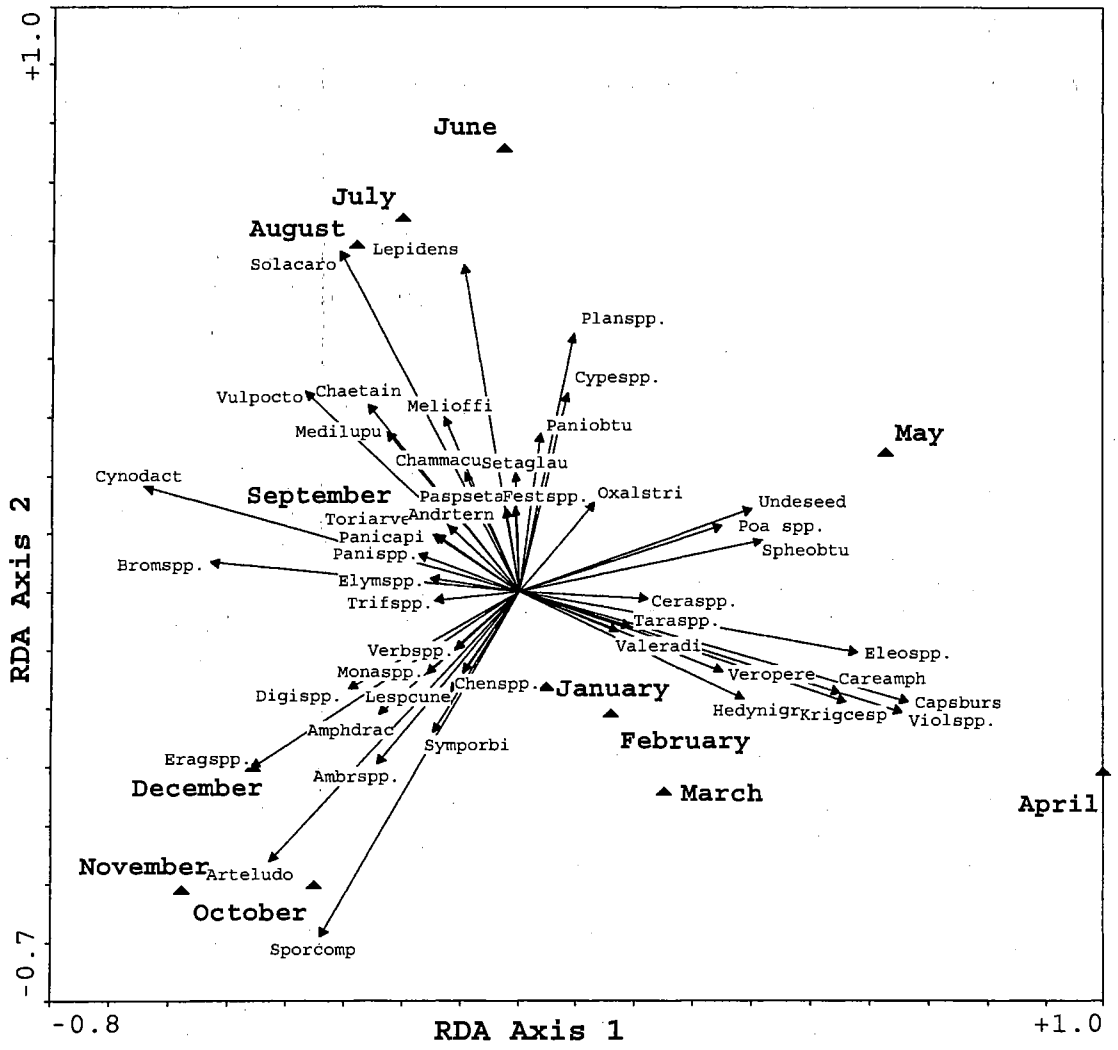

Number of seeds/g of dung DM
12
10
8
6
4
2
0
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
Month

Figure 4. Bi-plot showing the first two axes of RDA of seed species found in bison dung across seasons. Centroids (represented by triangles) of nominal explanatory variables (months) are plotted with species, represented by arrows. Ambrspp.: *Ambrosia* spp.; Amphdrac: *Amphiachyris dracunculoides*; Andrtern: *Andropogon ternarius* ; Arteludo: *Artemisia ludoviciana* ; Bromspp.: *Bromus* spp.; Capsburs: *Capsella bursa -pastoris*; Careamph: *Carex amphibola* ; Ceraspp.- *Cerastium* spp.; Chaertain - *Chaerophyllum tainturieri* ; Chammacu - *Chamaesyce maculata*; Chenspp.- *Chenopodium* spp.; Cynodact- *Cynodon dactylon*; Cypespp.- *Cyperus* spp.; Digispp.- *Digitaria* spp.; Eleospp. - *Eleocharis* spp.; Elymspp. - *Elymus* spp.; Eragspp. - *Eragrostis* spp.; Festspp. - *Festuca* spp.; Hedynigr - *Hedyotis nigricans*; Krigcesp - *Krigia cespitosa*; Lepidens - *Lepidium densiflorum* ; Lespcune - *Lespedeza cuneata* ; Medil upu- *Medicago lupulina* ; Melioffi - *Melilotus officinalis*; Monaspp. - *Monarda* spp.; Oxastri - *Oxalis stricta*; Panicapi- *Panicum capillare*; Paniobtu- *Panicum obtusum*; Panispp.- *Panicum* spp.; Paspseta- *Paspalum setaceum*; Planspp.- *Plantago* spp.; Poaspp.- *Poa* spp.; Setaglau- *Setaria glauca*; Solacaro- *Solanum carolinense*; Spheobtu- *Sphenopholis obtusata*; Sporaspe- *Sporobolus compositus* ; Symporbi - *Symphoricarpos orbiculatus* ; Taraspp. - *Taraxacum* spp.; Toriarve- *Torilis* arvensis; Trifspp. - *Trifolium* spp.; Undeseed - Un dentified seed; Valeradi- *Valerianella radiata* ; Verbspp. - *Verbena* spp.; Veropere - *Veronica peregrina* ; Violspp.- *Viola* spp.; Vulpocto- *Vulpia octoflora*.


+1.0
-0.7
RDA Axis 2
-0.8
RDA Axis 1
+1.0
June
July
August
Lepidens
Solacaro
Planspp.
Cypespp.
Vulpocto
Chaetain
Melioffi
Paniobtu
Medilupu
May
Chammacu
Setaglau
Cynodact
September
Paspseta
Festspp.
Oxalstri
Undeseed
Toriarve
Andrtern
Poa spp.
Panicapi
Spheobtu
Panispp.
Bromspp.
Elymspp.
Trifspp.
Ceraspp.
Taraspp.
Verbspp.
Valeradi
Eleospp.
Monaspp.
Veropere
Careamph
Chenspp.
January
Digispp.
Lespcune
Hedynigr
Krigcesp
Capsburs
Violspp.
Amphdrac
February
Symporbi
Eragspp.
Ambrspp.
December
March
April
November
Arteludo
October
Sporcomp

CHAPTER III

BEHAVIORAL COMPARISONS BETWEEN BISON (*Bison bison*) AND CATTLE (*Bos taurus*) ON SOUTHERN PLAINS

Abstract- Grazing and active behaviors of bison and cattle were compared across seasons in a tallgrass prairie and the effects of ambient temperature on behaviors were examined. Diurnal active behavior was affected by season and temperature, but not by species. Diurnal grazing behavior was affected by season, ambient temperature, and species. During the day bison spent less time grazing than cattle during winter, spring, and summer 2002, spent more time grazing than cattle during fall, and did not differ from cattle in grazing activity in summer 2001. Nocturnal grazing was affected by season, ambient temperature and species. Bison spent more time grazing at night than cattle in all seasons except during spring. The results suggest that the two species differed in the ways they cope with both high and low ambient temperatures during some periods of the year. Behavioral comparisons between the two species, grazing behavior in particular, should include nocturnal data collection.

Introduction

Historical accounts (Flores 1991) estimated that about 8 million bison once inhabited the southern plains of North America. Bison must have been exposed to high ambient temperatures in some southern parts of their range and could have developed behavioral or physiological adaptations to withstand high temperatures; however, bison were extirpated from their southern range before such important information about the species could be gathered. It is still unresolved whether or not bison were migratory in pre-Columbian times (Hart 2001). If bison migrated in response to climate thereby avoiding high ambient temperatures, physiological or behavioral adaptations to high temperatures would not be needed. Increasing ambient temperature was reported to affect bison behavior. Belovsky and Slade (1986) reported that daily activity time of bison decreases as mean daily air temperature increases. Hein and Preston (1998) observed that nocturnal grazing by bison was associated with both increased ambient temperatures and decreased precipitation, and suggested that nocturnal foraging could be a foraging strategy to conserve water during hot, dry periods. More recently, Maichak (2002) studied behavior of adult and juvenile bison in a tallgrass prairie of Oklahoma and observed that increases in ambient temperature reduced daily activity, particularly during summer.

Study of bison behavioral responses to ambient temperature at low latitudes would be more meaningful if compared with domestic cattle (*Bos taurus*), a closely related, similar-sized generalist ruminant that has replaced bison in most of their original distribution in the Great Plains. Bison and cattle were compared at high latitudes and the results showed that bison were less dependent on water and more mobile than cattle (Peden et al. 1974), and less selective foragers, allocating less time to grazing than cattle during the summer (Plumb and Dodd 1993).

The objective of this study was to compare behavior between bison and cattle across seasons and to determine how ambient temperature affects those behaviors. To accomplish these objectives the following null hypotheses were tested:

1) Diurnal grazing behavior of bison and cattle do not differ across seasons;
2) Daily activity behavior of bison and cattle do not differ across seasons;
3) Ambient temperature has similar effects on diurnal grazing behavior of bison and cattle across seasons;
4) Ambient temperature has similar effects on daily activity of bison and cattle across seasons;
5) Nocturnal grazing behavior of bison and cattle does not differ across seasons;
6) Ambient temperature has similar effects on nocturnal grazing behavior of bison and cattle.

Material and methods

Study Area

This study was conducted from August 2001 through July 2002 in the Tallgrass Prairie Preserve, owned by the Nature Conservancy, located in Osage County, Oklahoma (36°50′ 96°25′W). Mean local annual precipitation is 1010 mm and mean local daily temperatures vary from 1.6°C in January to 27.7°C in July (http://climate.ocs.ou.edu/county/osage.html).

Experimental Units

Three juvenile male bison and three English crossbred steers were used in this study. Bison and steers were 2.5 and 1.5 years old and weighed on average 365 and 347 kg, respectively, at the beginning of the experiment. Because I was interested in comparing behavioral responses of bison and cattle to ambient temperature and because heat exchange with the environment is size-related (Schmidt-Nielsen 1997), I compared animals with similar body weight instead of similar age. To facilitate identification, each animal was tagged before starting the study. During the study all animals were kept in the same enclosure (60.7 ha) where they foraged on natural tallgrass prairie vegetation and had free access to water from an artificial pond, and to mineral salts. For practical reasons, before the fall annual roundup was performed at the Tallgrass Prairie Preserve, the experimental animals were moved to a tall fescue pasture (*Festuca arundinacea*) (36.4 ha) inside the preserve, were kept

there during winter and early spring, and were returned to the original enclosure by mid-spring. At the tall fescue pasture the animals had access to hay, mineral salts, and water from an artificial pond.

Data collection and analysis

I collected behavioral data from bison and steers in 24-hour monitoring sessions during Summer 2001(n=7), Fall 2001(n=4), Winter 2002 (n=2), Spring 2002 (n=3), and Summer 2002 (n=3). The animals were followed by truck or by foot, and observed with 10 x 50 binoculars during the day. At night, I used spotlight and night vision monocular to locate the animals. I recorded individual behaviors at 15 to 30-minute intervals during the day and at 30-minute to 1-hour intervals at night or each time animals were located. The following activities were recorded: lying, standing, drinking, grazing, walking, running, rubbing, wallowing (exclusive of bison), and social interaction. Difficulties in following animals at night resulted in scarce nocturnal data recording. Because of that, diurnal and nocturnal data were analyzed separately.

I obtained ambient temperature (°C) data at 15-minute intervals for each day of data collection from the Oklahoma MESONET. The data were recorded at the Foraker MESONET station located inside the Tallgrass Prairie Preserve. On few occasions, when there were missing data on ambient temperature at the Foraker MESONET station, I averaged ambient temperatures of two

other MESONET stations (Burbank and Newkirk) near to the Foraker station for each missing data value.

I analyzed the diurnal data by logistic regression (GENMOD procedure of SAS) for grazing and active behaviors separately. I considered all behaviors as active except lying and standing, which were considered inactive behaviors, accompanied or not by rumination. I used season, ambient temperature, and species as explanatory variables. Since a previous analysis of summers 2001 and 2002 detected season differences, data from the two summers were not pooled. I analyzed the data with a saturated model with all double and triple interactions; when no significant interaction effects were found I used a reduced model. I used animal inside season*species in the REPEATED statement of GENMOD to account for repeated measures within animals, and subsequent tested within seasons. I used the option "type3" in the model statement of the GENMOD procedure to test the statistical significance of all main factors and interactions included in the model, and LSMEANS/diff option to test for differences between means. Nocturnal data for grazing behavior were analyzed in a similar way, only excluding data from summer 2001 due to an incomplete dataset.

Results

Diurnal grazing behavior

A total of 5784 diurnal behavioral observations were collected from both species in all seasons. Table 1 shows the

results of the statistical analyses of all seasons and each season individually. With the exception of the temperature*species interaction, all other effects were significant. Bison spent less time grazing than cattle in most seasons, but there was no difference in grazing activity between bison and cattle in summer 2001. The probability of grazing decreased in both species as ambient temperature increased (figure 1-A). During fall, bison were more likely to graze at low ambient temperatures than cattle, but bison grazing decreased more rapidly than cattle as ambient temperature increased. Increasing ambient temperature positively affected grazing behavior of bison and cattle during winter (figure 1-C) and spring (figure 1-D), but bison spent less time grazing than cattle in both seasons (table 1, figure 1). In summer 2002, both species decreased grazing activity as ambient temperature increased, but bison spent less time grazing than cattle at all ambient temperatures.

We rejected hypothesis 1 because grazing behavior of bison and cattle differed in all seasons, except in summer 2001. We also rejected hypothesis 3 because, at least during fall and summer 2002, bison and cattle responded differently to changes in ambient temperature.

Diurnal active behavior

Since species, temperature*species, and season*species effects were not significant (table 2), we accepted hypotheses 2

and 4 that diurnal active behavior did not differ between bison and cattle across seasons and that ambient temperature affected active behavior similarly in both species, respectively. Analysis of each season separately showed that increasing ambient temperature reduced activity in both species during the two summers and fall, and increased activity of both species during winter and spring.

Nocturnal grazing behavior

Nocturnal grazing analysis was based on 1570 observations collected in four seasons. All main and interaction effects included in the model were significant (Table 3), so hypotheses 5 and 6 were rejected. Bison spent more time grazing at night than cattle in all seasons except in spring (Table 3, Figure 2C). Increasing ambient temperature was positively associated with to grazing, except for bison during fall (Figure 2) and temperature*species interaction was significant in all seasons, except spring (Table 3, Figure 2C).

Discussion

Bison spent less time grazing than cattle during the day in all seasons, except in fall and summer 2001. These results agree with those of by Plumb and Dodd (1993) and reinforce the concept that bison are less selective than cattle (Peden et al. 1974). Time spent grazing was lower in spring, intermediate in summer and greatest in fall and winter for both species. These results

were similar to those found by Maichak (2002) for bison groups at the Tallgrass Prairie Preserve and seem to agree with both plant phenology at tallgrass prairie and animal metabolic requirements. During spring, when preferable forages (Coppedge and Shaw 1998) were more nutritious and less fibrous, animals would probably spend less time searching. As season progressed, plant productivity increased, but quality decreased, probably increasing animal selectivity. During fall and winter plant quality is low and metabolic demands of both species increase with decreasing ambient temperature (Christopherson et al. 1978). Even spending more time grazing during fall and winter, bison actually lose weight during this period in tallgrass prairie (Towne 1999) and cattle would also if they were not supplemented with protein, as commonly occurs in commercial cattle ranches in this region.

Fall was the only season when bison spent more time grazing than cattle and because bison are less selective than cattle (Peden at al. 1974). This difference in time spent grazing is possibly attributable to an increase in food intake, which could have been influenced by photoperiod. Photoperiod affects voluntary food intake in deer (Rhind et al.1998) and sheep (Clarke 2001). It is possible that bison responded to photoperiod by increasing food intake to put up fat reserves to survive winter. If cattle once showed the same characteristic during their evolution, this was probably lost in the process of intense artificial selection for productivity. The fact that bison are

seasonally polyestrous while cattle reproduce yearlong supports this conclusion.

Grazing behavior differed between summer 2001 and summer 2002. Figures 1A and 1E suggest that cattle grazing behavior was similar in both summers, but bison probability of grazing was lower in summer 2002 than in summer 2001, a result that lacks an obvious explanation. Ambient temperatures were similar in both summers (figure 3). My observations for summer 2002 seemed more similar to other bison behavioral studies than our observations for summer 2001. Bison spent less time (47%) grazing than cattle (51%) during summer in mixed prairie of South Dakota (Plumb and Dodd 1993). Maichak (2002) observed that adult bison spent about 40% of the time grazing during summer. Belovsky and Slade (1986) found that during late spring and summer in Montana, bison spent 46% of the time active and grazed only 12% of behaviors.

Although not included in the statistical analysis, some details of bison and cattle behaviors during the summer revealed different strategies used by each species to cope with heat stress that is reflective of their life history. Cattle evolved in woodlands and forested areas (Wuerthner 1997). During the hottest hours of the summer cattle rested under shade and near water, sometimes even standing in the pond. In contrast, plains bison evolved in grasslands and parklands and became adapted to open landscapes (Wuerthner 1997). During hot hours bison lay near the pond, went to the pond sometimes to drink, but never sought shade or immersed their bodies in water.

Bison spent more time grazing at night than cattle in all seasons, except in spring. This could lead us to speculate that bison do not graze less than cattle, but graze at different times. Before this study, all behavioral studies comparing bison and cattle were based on diurnal grazing only. Unfortunately, it is not possible to make any conclusion just from this study because diurnal and nocturnal data were collected at different intervals, and they were analyzed separately. So, no direct comparison can be made between the species in their total grazing time (diurnal plus nocturnal). Nevertheless, the results of this study indicate that grazing behavior comparisons between the two species should include nocturnal grazing data.

Increasing ambient temperature increased nocturnal grazing in all seasons except fall (Figure 2). Since ambient temperature decreases as daytime progresses in all seasons (Figure 3), this result could indicate that animals from both species are more likely to graze in the first hours of night and decrease grazing activity as night progresses.

Conclusions

When considering all seasons, bison spent less time grazing during the day than cattle. Ambient temperature affected both grazing and active behaviors of both species. In general, active and grazing behaviors of both species increased with an increase in ambient temperature during winter and spring and decreased with increasing ambient temperature in summer and fall. Nocturnal

grazing behavior was greater in bison than in cattle in all seasons, except spring. The fact that bison spent less time grazing than cattle during the day in some seasons and spent more time grazing at night than cattle in most seasons suggests that the species differ in their grazing strategies.

Acknowledgements

It would be not possible to conduct this study without the financial support given by Dr. David M. Engle. I am also grateful to Robert G. Hamilton from The Nature Conservancy for allowing me to perform this study and for giving support in each aspect of this work.

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Table 1. Type 3 tests generated by the GENMOD procedure for all effects included in the model for diurnal grazing behavior.

Source of variation	DF	χ^2	Pr> χ^2
All data			
season	4	27.83	<.0001
temperature	1	13.76	0.0002
species	1	12.94	0.0003
Temperature*season	4	21.89	0.0002
Season*species	4	14.08	0.0071
Temperature*species	1	1.51	0.2195
Temperature*season*species	4	12.58	0.0135
Summer 2001			
temperature	1	5.94	0.0148
species	1	1.85	0.1736
temperature*species	1	0.00	0.9691
Fall			
temperature	1	5.67	0.0173
species	1	4.39	0.0361
temperature*species	1	5.08	0.0241
Winter			
temperature	1	5.94	0.0148
species	1	4.90	0.0269
temperature*species	1	3.02	0.0820
Spring			
temperature	1	5.68	0.0172
species	1	4.17	0.0412
temperature*species	1	2.38	0.1227
Summer 2002			
temperature	1	5.64	0.0175
species	1	5.52	0.0188
temperature*species	1	4.38	0.0365

Table 2. Type 3 tests generated by the GENMOD procedure for all effects included in the model for diurnal active behavior.

Source of variation	DF	χ^2	Pr> χ^2
All data			
season	4	27.52	<.0001
temperature	1	10.54	0.0012
species	1	0.33	0.5652
Temperature*season	4	23.22	0.0001
Season*species	4	7.20	0.1257
Temperature*species	1	1.04	0.3089
Temperature*season*species	4	8.82	0.0658
Summer 2001			
temperature	1	5.90	0.0152
species	1	0.75	0.3869
temperature*species	1	1.83	0.1766
Fall			
temperature	1	5.46	0.0194
species	1	2.78	0.0954
temperature*species	1	3.87	0.0491
Spring			
temperature	1	5.71	0.0169
species	1	1.77	0.1833
temperature*species	1	0.45	0.5024
Winter			
temperature	1	5.91	0.0151
species	1	3.56	0.0591
temperature*species	1	3.05	0.0810
Summer 2002			
temperature	1	5.71	0.0169
species	1	1.11	0.2912
temperature*species	1	0.17	0.6774

Table 3. Type 3 tests generated by the GENMOD procedure for all effects included in the model for nocturnal grazing behavior

Source of variation	DF	χ^2	Pr> χ^2
All data			
season	3	17.06	0.0007
temperature	1	18.84	<.0001
species	1	8.72	0.0031
Temperature*season	3	20.25	0.0002
Season*species	3	12.22	0.0067
Temperature*species	1	15.45	<.0001
Temperature*season*species	3	10.50	0.0148
Fall			
temperature	1	0.44	0.5085
species	1	5.77	0.0163
temperature*species	1	5.43	0.0198
Winter			
temperature	1	5.83	0.0158
species	1	5.16	0.0231
temperature*species	1	4.54	0.0331
Spring			
temperature	1	5.53	0.0187
species	1	2.27	0.1319
temperature*species	1	0.50	0.4779
Summer 2002			
temperature	1	5.74	0.0165
species	1	5.48	0.0193
temperature*species	1	5.43	0.0198

Figure 1. Probability of diurnal grazing of bison (solid line) and cattle (dashed line) relative to ambient temperature (°C) generated by the logistic regression model for each season. **A**- Summer 2001; **B**- Fall; **C**- Winter; **D**- Spring; **E**- Summer 2002.

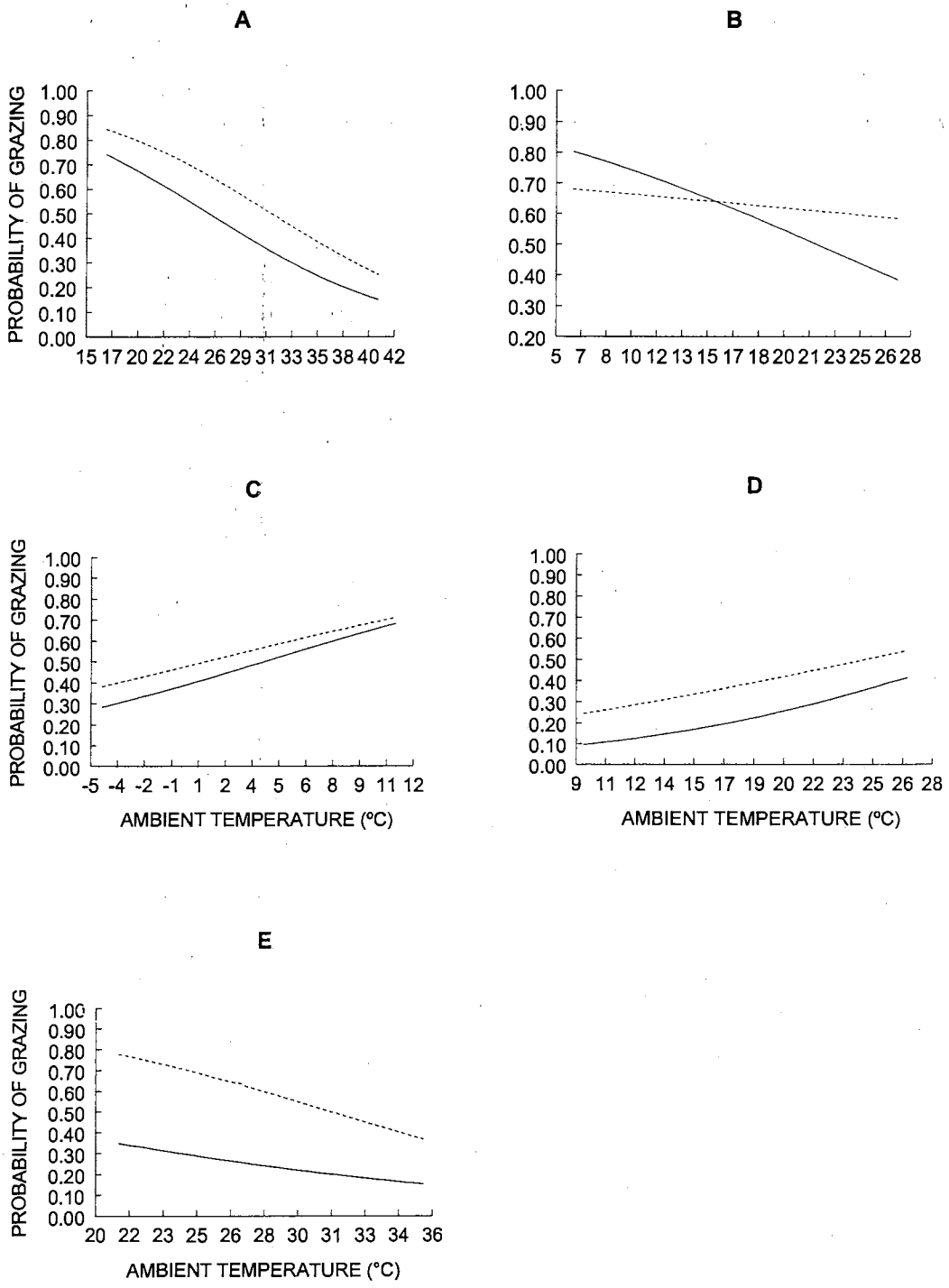

A
B
C
D
E
PROBABILITY OF GRAZING
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
15 17 20 22 24 26 29 31 33 35 38 40 42
5 7 8 10 12 13 15 17 18 20 21 23 25 26 28
-5 -4 -2 -1 1 2 4 5 6 8 9 11 12
9 11 12 14 15 17 19 20 22 23 25 26 28
20 22 23 25 26 28 30 31 33 34 36
AMBIENT TEMPERATURE (°C)

Figure 2. Probability of nocturnal grazing of bison (solid line) and cattle (dashed line) relative to ambient temperature (°C) generated by the logistic regression model for each season. **A**- Fall; **B**- Winter; **C**- Spring; **D**- Summer 2002.

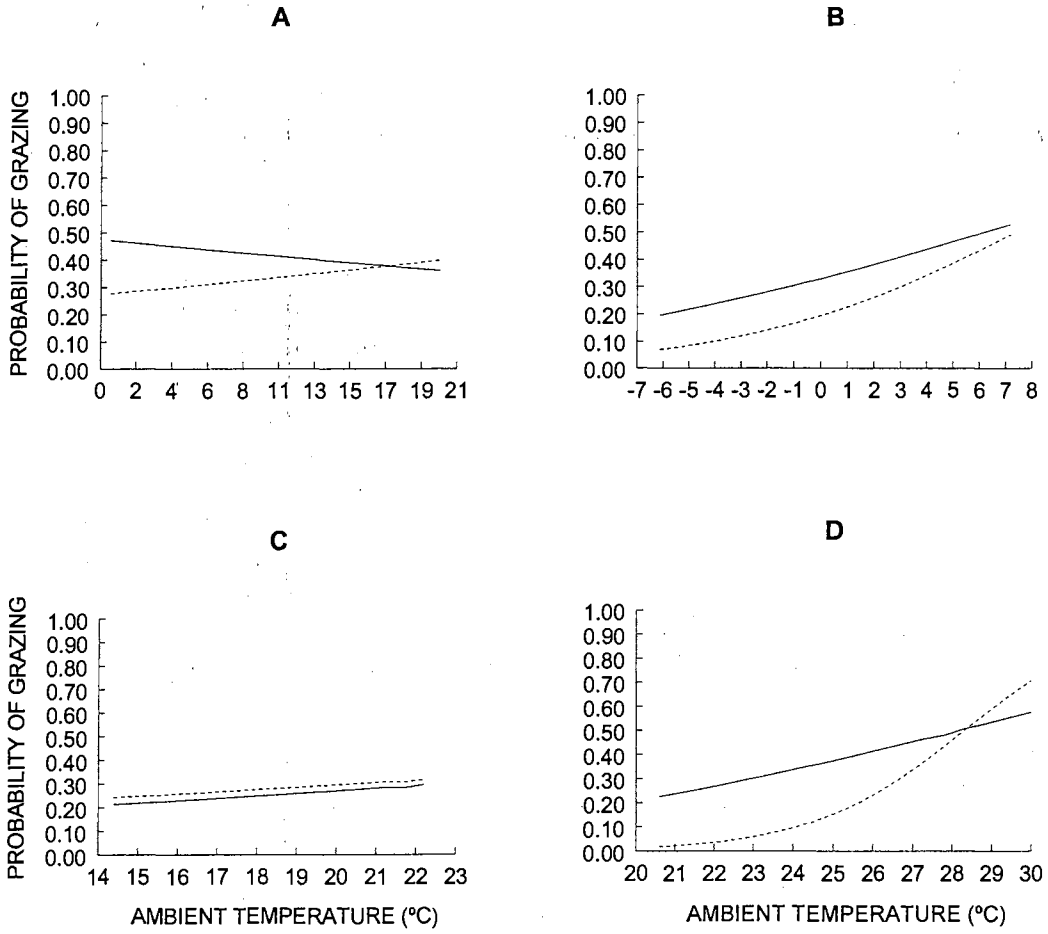
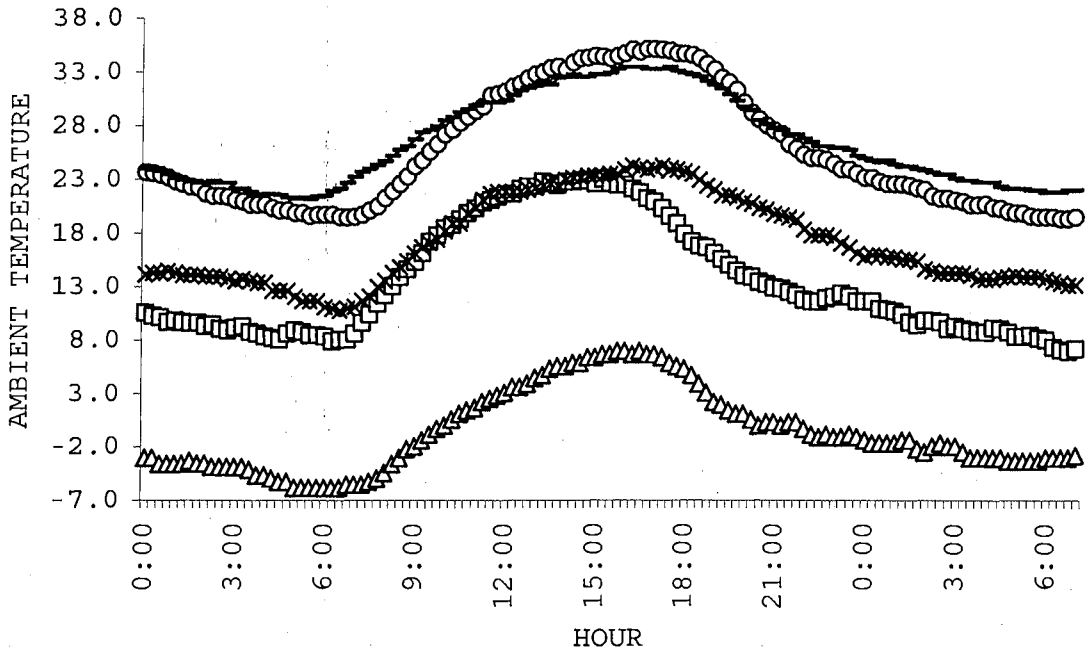

A
B
C
D
PROBABILITY OF GRAZING
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
0 2 4 6 8 11 13 15 17 19 21
-7 -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 7 8
14 15 16 17 18 19 20 21 22 23
20 21 22 23 24 25 26 27 28 29 30
AMBIENT TEMPERATURE (°C)

Figure 3. Ambient temperature (°C) averaged by season for all monitoring sessions (recorded at 15-minute intervals). Summer 2001 (○), Summer 2002 (-), Fall (□), Winter (Δ), Spring (x).


AMBIENT TEMPERATURE
38.0
33.0
28.0
23.0
18.0
13.0
8.0
3.0
-2.0
-7.0
0:00
3:00
6:00
9:00
12:00
15:00
18:00
21:00
0:00
3:00
6:00
HOUR

CHAPTER IV

SEXUAL SEGREGATION AND SEX RATIO IN BISON (*Bison bison*) AND POTENTIAL IMPACT ON NORTH AMERICAN GREAT PLAINS PRAIRIES

ABSTRACT. – I measured carbon isotopes in bison hair to determine if adult male and female bison differ in their diet composition in a tallgrass prairie ecosystem. Results were integrated with information about bison sex ratios in some public and private herds in the Great Plains and behavioral differences between sexes from the literature to discuss the possible effects different sex ratios could have on vegetation structure and/or composition and patchiness across the landscape. Carbon isotope analyses confirmed that diet of adult male bison differs from adult female and juvenile bison in Tallgrass Prairie Preserve. Bison sex ratios in about half of the herds are highly skewed toward females. The majority of studies in the Great Plains addressing the effects of bison grazing did not consider behavioral differences between sexes. Due to behavioral differences between adult male and female bison, different sex ratios in bison herds may result in different vegetation

structure and composition and patchiness of the landscape.

Introduction

Bison (*Bison bison*) (Larson 1940, Stebbins 1981, Knapp et al. 1999), in combination with fire and drought (Axelrod 1985), were major forces shaping Great Plains prairie ecosystems. For this reason, bison have been reintroduced to remaining tracts of prairies in the Great Plains to restore biodiversity (Hamilton 1996, Hartnett et al. 1996, Truett et al. 2001). However, when considering the use of bison as an ecological tool, some important behavioral differences within this species may have been underestimated.

Bison, like many other ungulates, show sexual segregation most of the year, except during the rut. This characteristic is believed to have been part of bison biology for at least 35,000 years (Berger and Cunningham 1994). Because of sexual segregation, adult males may differ from females in habitat selection (Berger and Cunningham 1994, Coppedge and Shaw 1998a), group size (Berger and Cunningham 1994, Schuler 2002), diet composition (Coppedge and Shaw 1998b, Post et al. 2001), and mobility (Berger and Cunningham 1994, Schuler 2002). Considering this information and the fact that bison population numbers in the Great Plains are artificially managed instead of controlled by natural processes, I was interested in comparing their sex ratios. Due to sexual segregation, adult male and female bison can differ in their impacts on vegetation structure and

composition and patchiness. Because of that, different sex ratios in bison would generate different levels of disturbances across the landscape.

The objectives of this study were to 1) determine if adult male bison differ from females and juveniles in their diet composition in the tallgrass prairie, and 2) review sex ratios from bison herds in parks, preserves and refuges, and to discuss their possible effects on the restoration and conservation of grasslands in the Great Plains.

Methods

I used free-ranging adult and juvenile bison of both sexes from the Nature Conservancy's Tallgrass Prairie Preserve (TGPP), Osage Hills of northern Oklahoma (36°50'N, 96°25'W). At the time of data collection, the bison herd of TGPP consisted of 78 (2001) bulls (≥3.5 yrs-old), 492 (2001) cows (≥3.5 yrs-old), 419 (2001) juveniles (>1 and ≤2.5 yrs-old), and 370 calves (<1 yr-old). The animals have free access to the entire bison unit, which has been expanded progressively concomitant with the expansion of the bison herd to maintain a stocking density of 6-7 ha AU^{-1} (Coppedge and Shaw 1998a). Although bison had free access to salt with trace minerals, they did not receive supplemental feed at any time (Hamilton 1996). Approximately one third of the preserve is burned every year in randomly selected patches in early spring, summer and fall (Hamilton 1996).

During the roundup of November 2001, animals were individually constrained in a squeeze chute and hair samples were collected from each animal's head using an electric clipper. The origin and age of each animal were identified by transponders carried by each animal. I used hair samples only from animals that were born at the TGPP. I cut small pieces from the base of the hair, loaded them into tin cups (≈100mg), and sent them to the Department of Biology, University of Utah to have stable isotopes of carbon analyzed. The ratio of stable isotopes is expressed in δ notation in parts per thousand where

$$\delta^{13}C\ (‰) = ((^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{standard}) - 1) \times 1{,}000)$$

The standard used for $\delta^{13}C$ was Peedee belemnite marine limestone (PDB). The ratios of stable carbon isotopes have been used successfully to indicate the diet type of herbivores due to the difference in ^{13}C isotope content between C_3 and C_4 plants. This difference is derived from the discrimination against ^{13}C isotopes made by the primary CO_2-fixing enzyme of C_3 plants and it is reflected in the consumer tissues (Kelly 2000). For statistical analysis I divided the animals in three groups: bulls (≥3.5 years-old), cows (≥3.5 years-old), and juveniles (animals from both sexes ≥1 and ≤ 2.5 years-old). All statistical procedures were performed using Statistical Analysis Software (SAS Institute Inc. 2001). I tested data for homogeneity of variance using Levene's test ($F=1.38$, $p=0.2664$) and for normality using Shapiro-Wilk test ($Pr<W= 0.1519$). I analyzed the data by

analysis of variance (PROC GLM procedure), and I used least-square-difference test to detect differences in diet content among groups at α=0.05.

To obtain information about sex ratios in bison herds accessible to the public, I contacted parks, preserves and refuges in the Great Plains where bison are known to be present according to the National Bison Association website (http://www.bisoncentral.com/nba/mission.asp). The information gathered is presented on Table 2.

Results

There was a difference between groups in relation to the ^{13}C:^{14}C stable isotope ratios present in hair (F= 7.16, p= 0.0019). Carbon isotope ratios differ between bulls and cows (p= 0.0470), bulls and juveniles (p= 0.0005), and between cows and juveniles (p=0.0315). Table 1 shows the mean $\delta^{13}C$ for each group. Sex ratios were highly skewed toward females (Table 2) in about half of the establishments contacted in the Great Plains where bison were known to be present.

Discussion

Botanical composition of diets

The average $\delta^{13}C$ values for C_3 and C_4 plants are -26.5 and -12.5‰, respectively (Chisholm et al. 1985). Considering a mean ^{13}C isotope enrichment of 3.1‰ between keratin (horn, hoof, and hair) and diet in large ruminants (Cerling and Harris 1999), I can

roughly estimate $\delta^{13}C$ values for diets of bulls, cows, and juveniles in the Tallgrass Prairie Preserve (TGPP) of about -15.7, -16.5, and -17.2‰, respectively. These values are similar to those found by Tiezen et al. (1998) in bison dung in the TGPP ($\delta^{13}C$=-16.8). The $\delta^{13}C$ values obtained from bison hair indicate that bison at tallgrass prairie consume essentially C_4 plants as has been reported before (Coppedge and Shaw 1998b), but also show that the proportion of C_4 plants in diet is highest in bulls, intermediate in cows, and lowest in juveniles. Since C_3 plants are higher in dry matter digestibility than C_4 plants, I can conclude that in the tallgrass prairie the quality of diet is highest for juveniles and lowest for bulls, at least in fall.

My results are similar to those reported by Post et al. (2001) who measured carbon isotopes monthly in bison dung and found that bulls have lower diet quality than cows, juveniles, and calves in the Konza Prairie Research Natural Area. However, in my study the diet of cows was higher in C_4 plants than was that of juveniles. These results contrast with those obtained by Post et al. (2001), in which the diet of cows and juveniles were similar throughout the year, except during April, when the content of C_3 plants in juveniles' diet was higher than in cows' diet. I collected my samples during a period when there was a peak in consumption of C_3 plants by bison in the tallgrass prairie (Tiezen et al. 1996, Coppedge and Shaw 1998b, Post et al. 2001). It is possible that Post et al. (2001) could not detect

differences between cows and juveniles during the same period in the Konza Prairie Preserve due to the small sample size.

Juvenile bison from both sexes remain in female groups. Because juveniles and cows inhabit the same habitat, differences in diet composition between them could be explained by a greater grazing selectivity by juveniles. If so, then juveniles should spend more time grazing than cows. However, the only study carried out in the Tallgrass Prairie Preserve (TGPP) that compared time budget between adult and juvenile bison across seasons did not find any difference between them in time spent grazing (Maichak 2002). However, Maichak (2002), possibly to facilitate identification, considered adults those animals ≥ 1 yrs-old, and juveniles animals < 1 yr-old, while in this study and I considered adults only animals ≥ 3 yrs-old.

Segregation and herd composition

My results show that diets of adult male and female bison in the tallgrass prairie have different proportions of C_3 and C_4 plants. Sexual segregation and differences in diet composition between adult male and female bison could result in different impacts on vegetation structure and/or composition in the tallgrass prairie ecosystem. Previous studies carried out in the Tallgrass Prairie Preserve (TGPP) (Coppedge and Shaw 1998a, Schuler 2002) demonstrated the interaction between bison and fire in shaping vegetation structure and composition. Bison are attracted to and graze preferentially recently burned patches (Coppock and Detling 1986, Shaw and Carter 1990, Coppedge and

Shaw 1998a, Biondini et al. 1999, Schuler 2002), at least during the growing season. This particular behavior results in a heterogeneous use of the landscape, with some areas under high grazing pressure and others under light grazing pressure or no grazing at all.

Not only do adult male and female bison segregate outside the rut, but they also differ in group size (Schuler 2002, Berger and Cunningham 1994, Komers et al. 1993). In the tallgrass prairie adult male bison form small groups, while females and their young form groups that vary in mean size from 23.3 in autumn and winter to 205.6 individuals in summer (Schuler 2002). Large groups formed during summer are generally mixed groups, when adult males join female groups. Female groups are comprised of adult females, their young, and juvenile male and female bison (Berger and Cunningham 1994, Schuler 2002). Considering that male groups are smaller in size than female groups, one could speculate that at a sex ratio 1:1 (M:F), males would be more evenly distributed across the landscape than females. Therefore, male and female bison would differ in their impacts on the landscape. If so, then one could expect different spatial vegetation structure and/or composition at different sex ratios of adult male and female bison at a specific stocking rate.

However, if the major impact of bison on the structure and/or composition of tallgrass prairie is mainly due to grazing recent burned patches during spring and summer, then the effect sex ratio would have on vegetation structure and composition

would be negligible and would have no relevance to the management and conservation of tallgrass prairie ecosystem. This would occur if the majority of adult males join cow-calf groups during the growing season. Although there is some evidence that bulls join cow-calf groups until 2-3 months before rut (Schuler 2002) in Tallgrass Prairie Preserve (TGPP), there is also evidence that at least some bulls do not do so, since bull groups were observed to exist throughout the year (Coppedge and Shaw 1998a, Schuler 2002). Nevertheless, it is not possible to make any conclusion about this issue because those studies were performed in a population in which males represented less than 20% of the adults. It is not known if the behavior of adult male bison is affected as their proportion increases or decreases in the population.

Berger and Gompper (1999) reviewed sex ratios in extant ungulates and observed that adult sex ratios generally favors females. However, for bison, the authors found in the literature male:female ratios for bison in presence or absence of predators ranging from 0.81 to 0.98, ratios that do not depart strongly from 1. Sex ratios were highly skewed toward females (Table 2) in about half of the preserves established in the Great Plains where bison were reintroduced as a disturbance force to restore biodiversity. In herds still expanding, having more females has the advantage of increasing herd numbers more rapidly, with the possibility of selling excess animals, and also avoids managing a large number of potentially dangerous mature bulls. However, the

majority of herds with skewed sex ratios had already reached a stable size. These bison herds are generally rounded up once a year and an artificial culling is performed. In the TGPP, not only the sex ratio greatly favors females, but also males ≥ 6 yrs-old are culled due to difficult of handling them.

Conclusions

Bison herds with skewed sex ratios disturb prairies of Great Plains differently from those of pre-settlement times. High densities of females would probably have a greater impact on recent burned sites than would be expected and very low density of males would be not sufficient to change vegetation structure and/or composition on sites inhabited preferentially by them. Although I have focused my attention on the possible impacts of skewed sex ratios of bison herds in the tallgrass prairie ecosystem, the same reasoning should be applied to other prairie ecosystems in the Great Plains where bison were reintroduced since sexual segregation is a common feature of bison populations irrespective the habitat type. I suggest those parks, preserves, and refuges with highly skewed sex ratios consider shifting to sex ratios closer to those found in bison wild populations.

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TABLE 1

MEAN $\delta^{13}C$ AND S.E.M. FOR BULLS, COWS, AND JUVENILES

Group	N	Mean $\delta^{13}C$ (‰)*	S.E.M.
Bulls	7	-12.6^{a}	0.32
Cows	15	-13.4^{b}	0.21
Juveniles	14	-14.1^{c}	0.22

* Means with different superscripts are different at α=.05.

TABLE 2

BISON HERD SIZES, SEX RATIOS, AND STATUS IN GREAT PLAINS' PARKS, PRESERVES AND REFUGES

Local	Herd Size Adults[a] (total)	Sex Ratio (M:F)	Area[b] (acres)	Herd status
Badlands National Park	452(755)	1.4:1	64,000	stable
Cross Ranch Preserve	42(86)	1:9.5	3,040	stable
Custer State Park	(950)	1:6.9	17,640	stable
Konza Prairie N.A.	175(280)	1:5.26	8,616	increasing
National Bison Range	203(404)	1:1.14	18,750	stable
Niobrara V. Preserve	171(383)[c]	1:13.3	7,500	stable
	132(281)	1:10	12,00	
Ordway M. Prairie	189(267)	1:9.5	3,000	stable
Tallgrass P. Preserve	570(1359)	1:6.3	10,486	increasing
Theodore Roosevelt	115(230)[c]	1:0.98	24,070	stable
National Park	129(263)	1:1.05	46,128	
Wichita Mountains W.R.	400(600)	1:1	60,000	stable
Wind Cave N. Park	255(475)	1:1.68	28,250	stable

[a] - animals ≥ 3 yrs-old

[b] - area accessible to bison

[c] - two herds in separate areas

CHAPTER V

BISON PRODUCTIVITY ON TALLGRASS PRAIRIE: A COMPARISON WITH OTHER GREAT PLAINS' HERDS

ABSTRACT - I analyzed productivity data of the bison herd on the Tallgrass Prairie Preserve and compared them with bison productivity data found in the literature. Bison calving rates at Tallgrass Prairie Preserve varied between 67 to 81% from 1995 to 2001, and calf sex ratios did not depart from 1:1 except in 1999. Males were heavier than females at all ages except at 6 months of age. Growth rate in both male and females bison was maximum (about 80%) between 0.5 to 1.5 years of age, and dropped to about half of that in the age interval between 1.5 to 2.5 years old. Growth rate of males differed at all age intervals, and males were still growing until 6.5 years old. Female growth rates from 4.5 to 5.5 years old and subsequent age intervals were similar indicating that females reached adult weight at about 4.5 years old. Bison productivity at Tallgrass Prairie Preserve seems to be in the range found in other nonsupplemented Great Plains herds. These findings are in opposition to the idea that bison were scarce in tallgrass prairie because of nutritional inadequacy.

Introduction

According to historical accounts (Shaw and Lee 1997), bison were far less abundant on tallgrass than on mixed grass or shortgrass prairies. Among the potential explanations for the scarcity of bison on tallgrass regions is inadequate nutritional quality during winter (Shaw and Lee 1997), particularly nitrogen deficiency (Botkin 1995). If so, then productivity of bison on tallgrass prairie should be lower than those of other prairie ecosystems under similar management. However, analyses of bison dung in four preserves owned by The Nature Conservancy located in mixed and tallgrass prairies showed that fecal nitrogen was low in all preserves, but was highest during early season at Konza Prairie and at Tallgrass Prairie Preserve, both tallgrass prairie regions (Tiezen et al. 1997). Towne (1999) analyzed productivity of a relatively small bison herd (n=200) in Konza Prairie, but his comparisons with other bison herds were generalized, not focused in differences of performance between prairies regions.

The objective of this study was to analyze productivity of the bison herd from the Tallgrass Prairie Preserve, Oklahoma, and to compare it with bison productivity data from other Great Plains herds found in the literature.

Material and Methods

Study Area

The Tallgrass Prairie Preserve, owned by The Nature Conservancy, is located in Osage County, Oklahoma (36°50'N

96°25'W). Big bluestem (*Andropogon gerardii*), indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*) and little bluestem (*Schyzachyrium scoparium*) dominate the vegetation of the area. Bison were reintroduced to the area as a disturbance force to recreate, in combination with seasonal patch burns, heterogeneity in vegetation structure and composition at landscape level.

Bison herd origin and management

The bison herd of the Tallgrass Prairie Preserve started when 300 animals were introduced to the preserve in October 1993 (Hamilton 1996). The initial herd was donated from Kenneth Adams, a bison rancher who started his own herd in 1980's from a broad base of different herds. The herd continuously exchanges animals with other herds, and is not under selection pressure for any particular character. Culling of young males and females is performed randomly, mating in the herd occurs with no human interference, and the low proportion of adult males in relation to adult females can be partially compensated for by the culling of males older than 6.5 years old and the annual introduction of males from other herds. Although no genetic study was performed in the herd, all these facts suggest that the herd is not inbred. So, any possible discrepancies in calving rate or body weight between bison TGPP herd and other herds cannot be attributable to inbreeding depression occurring in the TGPP herd.

The herd has been increasing in size since its formation and is expected to reach a maximum size of 3,200 animals that

will occupy the 12,300 hectares of the preserve (Hamilton 1996). The area of the preserve available to bison (bison unit) has been adjusted gradually with the expansion of the herd to a stocking rate of 1.3 AUM per hectare (Hamilton 1996). The animals had access to the entire bison unit where salt with trace minerals was provided by free choice and water by natural stream flow and small stock ponds (Hamilton 1996). The herd did not receive supplemental feed at any time (Hamilton 1996).

Data collection and analyses

During each fall roundup animals were constrained individually in a squeeze chute and weighed on an electronic scale. Individuals were identified by electronic transponders implanted in their ears. Data available for analysis comprised bison weight data and calving rates from 1995 to 2001. Data of all years were used to calculate calving rates and sex ratios in the herd, however, to compare weights between sexes or among ages within sexes, I used only years where all age categories of interest were represented.

Since there was no control of individual cow productivity, no information of calving rates by cow-age category was available. I obtained calving rates by dividing the number of calves present at the period of the roundup by the number of cows ≥3 yrs old. I used Chi-square analysis (PROC FREQ in SAS) to compare calving rates between years and calf sex ratios within year.

To compare sexes at different ages I analyzed weight data as a factorial treatment structure, with sex (2) and age (6) as fixed factors and year as random (block) factor. The model included sex, age, year, double (sex*year, age* year) and triple (sex*age*year) interactions. Prior to the main analysis, weight data were tested for heterogeneity of variance using Levene's test in GLM procedure of SAS. Since heterogeneity of variance was detected, data were analyzed by analysis of variance with MIXED procedure of SAS, using the REPEATED statement and 'GROUP=sex*age' option to account for heterogeneous variance (Littell et al. 1996). The 'SLICE' option in the LSMEANS statement was used to compare sexes at each age class. Due to missing data for male weights in many years, I used only data from years 1999 to 2001 to compare sexes. All calves were assumed to be 6 months old at the roundup period, however all calves from both sexes ≤100 kg were considered late born and were excluded from the analysis. I chose to compare sexes between ages 0.5 to 5.5 years old since the number of 6.5 years-old males in the dataset was scarce and males >6.5 years old were absent at the preserve.

Within-sex analyses were performed separately. Growth rates (GR) were calculated for each sex as the proportion of increase in body weight for individuals at each age interval as:

GR= (body weight at age X - body weight at age X-1)/ body weight at age X-1

I analyzed growth rates for each sex separately by analysis of variance with the MIXED procedure of SAS, using the REPEATED statement and the 'GROUP=age' option to account for heterogeneous variance (Littell et al. 1996). I used growth rate at each age interval as fixed factor and year as block factor. I tested differences in growth rates between age intervals with Tukey multiple comparisons test. For males I used growth rates at age intervals of 0.5 and 1.5, 1.5 and 2.5, 2.5 and 3.5, 3.5 and 4.5, 4.5 and 5.5, and 5.5 and 6.5 years old. For females, in addition to the age intervals used in male analysis, I also used growth rates between ages 6.5 and 7.5, 7.5 and 8.5, 8.5 and 9.5, and 9.5 and ≥10 years old.

Results

The bison herd of the Tallgrass Prairie Preserve has been increasing in size at an average of 21.5% (13.7 to 29.9) per year since its formation. Between 1995 and 2001 the herd adult sex ratio (M:F) was on average 1:8.1 (6.3 to 10.5). Calving rates from 1995 to 2001 are showed in Table 1. Calving rates did not differ from 1995 to 1998 (χ^2=2.7936, df=3, p=0.4245) and between 1999 and 2000 (χ^2=0.0919, df=1, p=0.7617), but differed between 1995-1998 and 1999-2000 periods (χ^2=35.3527, df=1, p<0.0001). Calving rates of 1999 and 2000 also differed from that of 2001 (χ^2=8.9121, df=1, p=0.0028). Sex ratios (Table 1) did not depart from the expected 1:1, except in 1999, when significantly more females than males were born (χ^2=5.4019,df=1, p=0.0201).

Male and female bison differed in body weight at all ages except at 6 months old ($F=3.12$, $p=0.1273$), and weight differences increase with age (Figure 1).

Male and female growth rates at different age intervals are shown in Table 2. Male growth rate between 0.5 and 1.5 years old was 84%, dropped to 47% between 1.5 and 2.5 years old, and continued decreasing in subsequent age intervals. All comparisons of growth rates at different age intervals in males were significant, indicating that until 6.5 years male bison were still growing. Female growth rate was 79.5% in the 0.1-1.5 years-old age interval, decreased to 39.9% from 1.5-2.5 years old, and to 8% at age intervals of 2.5-3.5 and 3.5-4.5 years old. Female growth rates from 4.5 to 5.5 years old and subsequent age intervals were similar indicating that females reached adult weight at about 4.5 years old (Table 2).

Discussion

I estimated calving rates from the number of calves that were present at the roundup period, which might underestimate the actual calving rate. However, since predators of bison were absent from the Tallgrass Prairie Preserve for a long time, these estimations were probably close to the real calving rate. Because a small percentage of bison heifers calve at 2 years old (Shaw and Carter 1989, Green and Rothstein 1991) the exclusion of 2.5-yrs-old females from the calving rate calculation could have resulted in an overestimation of calving rates. However this

could be partially compensated for by the small percentage of heifers that first calve at 4 years old (Green and Rothstein 1991).

Bison calving rates can be quite variable depending on herd management and environmental factors. Calving rate in the mixed-grass prairie of the Wind Cave National Park, South Dakota varied between 74 to 86% for females between 3 to 11 years of age (Green and Rothstein 1991). Rutberg (1986) reported mean calving rate of 88.2% in the National Bison Range, Montana, and Shaw and Carter (1988) observed mean calving rate of 71.8% in Wichita Mountains National Refuge for 2 to 18 years-old females. Steuter and Hidinger (1999) reported high calving rates (mean 84%, range from 72% to 94%) for females between 2 to 10 years of age mixed-grass prairie of the Niobrara Valley Preserve, Nebraska.

In 1999 an outbreak of anaplasmosis occurred in the bison herd. Anaplasmosis is a hemolytic, ryckettsial disease of ruminants transmitted mainly by ticks that causes anemia and consequent weight loss, abortion of pregnant animals, and even death (Stokka et al. 2000). The most apparent consequences to bison productivity in the TGPP were a significant drop in calving rate and a higher number of female than male calves born that year (Table 1). This suggests that there was a differential fetal loss caused by the disease. Juvenile males in dimorphic species are known to grow faster and consequently are more vulnerable to food restrictions than females (Clutton-Brock et al. 1985). Kruuk et al. (1999) observed that sex ratios in red

deer (*Cervus elaphus*) changed with population density, with fewer males being born from dominant females with increasing population density. Kruuk et al. (1999) suggested that male vulnerability to nutritional stress also could be extended to fetal development and that the change in sex ratio in deer at high population density was a result of male fetal loss. The reduced calving rate accompanied by a skewed calf sex ratio favoring females that occurred in the TGPP bison herd in 1999 could have been a consequence of an increase of fetal loss of male embryos. The herd was treated for anaplasmosis in 1999, but in 2000 the calving rate was still low, although no difference in the proportion of male and female calves was found that year. This is probably because in year 2000 animals that were affected by anaplasmosis were still recovering from the weight loss resulting in failures of conception rather than post-conception losses.

Table 3 shows bison weights at different ages found in the literature for bison herds located in the Great Plains. I also included weight data from some commercial ranches (raise bison for beef production) in Canada (Rutley et al. 1997) to give an idea of bison weights in supplemented and intensive managed herds. What is apparent in Table 3 is that bison weight can be quite variable, but bison weight data from TGPP do not seem to depart from those of other herds. As would be expected bison weight at TGPP is lower than those from commercial herds, but all other nonsupplemented herds seem also to have lighter animals than commercial herds. Berger and Peacock (1988) did not find

differences between bison body weights from National Bison Range (NBR) and Fort Niobrara National Wildlife Refuge (FNNWR). However, males from NBR seem to be heavier than those from FNNWR (Table 3). Probably the cause for that was the great variability they found among years at each location. Overall, weights from both male and female seem to be quiet variable from place to place.

The mean weight of females of ≥ 4 years old ranged between 400 to 425 kg, except Wichita Mountains that had lower values, and commercial ranches that have higher values. Green and Rothstein (1991) observed a trade-off between growth and productivity in female bison. Heavier yearling female bison started reproducing earlier (calved at 2 years old) than lighter ones, but at maturity these animals weighed less than animals that had their first calf at 3 years old (Green and Rothstein 1991). Although lighter when adults, precocious females produced more calves during their lifetime than heavier adult females, indicating that calving rate is a better indicator of cow productivity than adult body weight.

Conclusions

Genetic and environmental factors influence animal production. In this study I analyzed bison productivity data from the TGPP and compared with those of other bison herds found in the literature. I found that bison productivity is variable among locations, but bison productivity at TGPP seems to be in the

normal range found in other nonsupplemented bison herds in the Great Plains. Although it was not possible to compare locations statistically, the results of this study suggest that if bison were not abundant on tallgrass prairie in pre-settlement times, it was not due to nitrogen or other nutritional deficiencies.

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Table 1

CALVING RATES AND CALF SEX RATIOS AT THE TALLGRASS PRAIRIE PRESERVE BASED ON ANIMALS PRESENT AT THE FALL ROUNDUP FROM 1995 TO 2001

Year	Calving rate(%)[ac]	Number male calves	Number female calves
1995	75.5[d]	56	61
1996	81.4[d]	90	72
1997	80.6[d]	88	107
1998	81.8[d]	109	115
1999	67.9[e]	90*	124*
2000[b]	66.8[e]	146	148
2001	75.2[f]	196	174

a- based on number of ≥3 yrs-old females

b- calving rate calculation included five calves that were released before sex identification

c- calving rates with different superscript differed at α=0.05.

*- departed from 1:1 ratio at α=0.05

TABLE 2

MEAN GROWTH RATES AND STANDARD ERRORS FOR MALE AND FEMALE BISON AT DIFFERENT AGE INTERVALS (VALUES WITHIN COLUMNS WITH DIFFERENT SUPERSCRIPT DIFFER AT α=0.001)

Age interval	Male	S.E.M.	Female	S.E.M.
0.5-1.5	0.84^{a}	0.026	0.795^{a}	0.019
1.5-2.5	0.47^{b}	0.017	0.399^{b}	0.016
2.5-3.5	0.21^{c}	0.014	0.08^{c}	0.017
3.5-4.5	0.16^{d}	0.013	0.08^{c}	0.017
4.5-5.5	0.1^{e}	0.013	0.036^{d}	0.017
5.5-6.5	0.05^{f}	0.015	0.015^{d}	0.017
6.5-7.5	-	-	0.015^{d}	0.017
7.5-8.5	-	-	0.02^{d}	0.017
8.5-9.5	-	-	0.017^{d}	0.017
9.5-10.5*	-	-	0.005^{d}	0.017

*- data pulled for growth rates for age intervals of females >10 years old.

TABLE 3

MALE AND FEMALE BISON WEIGHTS AT DIFFERENT AGES FROM BISON HERDS IN THE GREAT PLAINS

Bison herd	Age (years)					
	0.5	1.5	2.5	3.5	4.5	5.5
Males						
National Bison Range[a]	-	-	310	460	580	680
Fort Niobrara N.W.R.[a]	-	-	280	370	430	500
Wichita Mountains N.W.R.[b]	-	281	364	436	511	536
Wind Cave National Park[c]	140	233	407	-	-	-
Konza Prairie N.R.A.[d]	134	260	380	490	550	650
Tallgrass Prairie P.[e]	160	285	422	523	613	683
Commercial ranches[f]	196	336	467	594*		
Females						
National Bison Range[a]	-	-	270	250	430	425
Fort Niobrara N.W.R.[a]	-	-	300	360	420	425
Wichita Mountains N.W.R.[b]	-	-	386	366	385	387
Wind Cave National Park[c]	138	235	376	413*	-	-
Konza Prairie N.R.A.[d]	124	240	340	380	400	415
Tallgrass Prairie P.[e]	150	256	356	387	409	419
Commercial ranches[f]	180	299	413	448*	-	-

a- Berger and Peacock, 1988; b- Halloran 1960; c- Green and Rothstein 1991; d- Towne 1996; e- this study; f- establishments that raise bison for beef production in Canada (Rutley et al. 1997)

*- body weights from adults (≥ 3.5 years old)

Note: Some weights were approximations made from visual examination of graphs instead of exact data (those from Bergman and Peacock 1998 and some from Towne 1996), since the precise data were not provided.

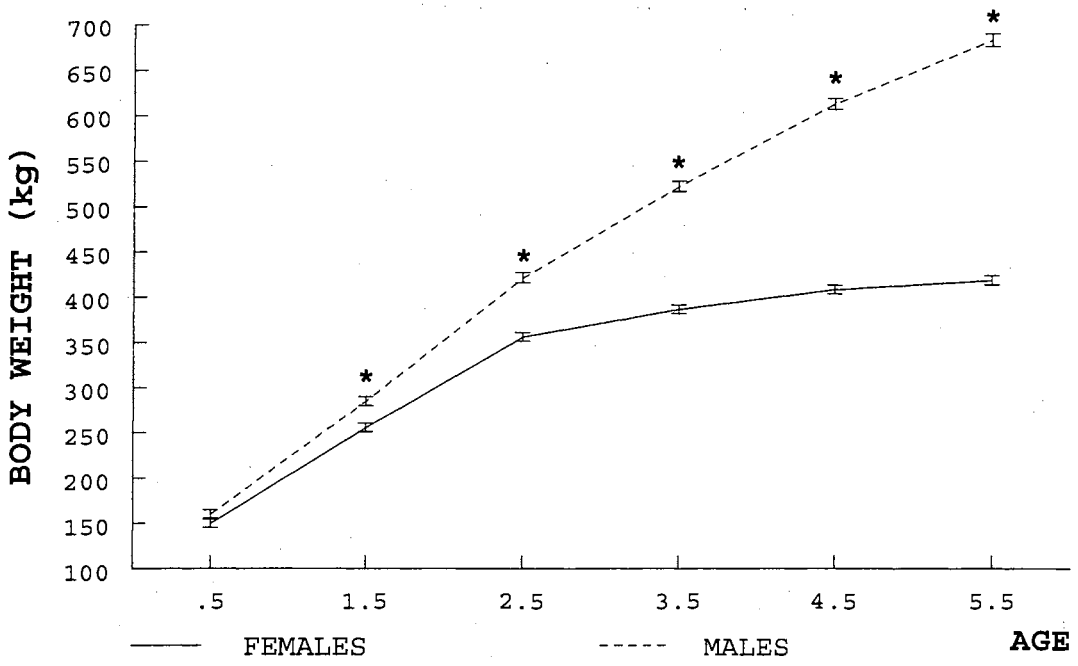

Figure 1. Male and female bison body weights (mean ± S.E.M.) at different ages at the Tallgrass Prairie Preserve. Male and female mean body weights with symbol '*' differed significantly at α= 0.05.

CHAPTER VI

SUMMARY

The large number of seeds from several species found in bison hair and dung attested to the role of bison as agent dispersers of seeds in the tallgrass prairie, both externally and internally. Graminoids represented 52.8% of the total number of seeds found in bison dung. The high number of forb seeds in bison dung contrasts with studies that showed that forbs comprised a small portion of bison diet. Although forbs maybe not make a great portion of bison diet, it seems that bison at least consume them in enough amounts and at phenological stages that promote their dispersal.

Bison and cattle active behaviors were affected similarly by ambient temperature across seasons, but not their grazing behaviors. Bison spent more time grazing during fall and less time grazing in summer than cattle. Nocturnal grazing behavior was greater in bison than in cattle in all seasons, except spring. Bison and cattle seem to have different grazing strategies.

Sex ratios were found highly skewed toward females in half of the preserves where bison were reintroduced to enhance

biodiversity and structural heterogeneity of the vegetation. Since adult male and female bison segregate most of the year and show differences in diet composition, it was suggested that sexes could impact the landscape differently. If so, herds with skewed sex ratios would result in different spatial or temporal vegetation heterogeneity than those found in herds with sex ratios that not strongly depart from 1:1.

Calving rates and sex ratios of bison herd of the Tallgrass Prairie Preserve seems to be in the range found in other unsupplemented herds in the Great Plains. These findings contrast with the theory that bison were scarce in tallgrass prairie regions due to nutritional deficiency.

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